

Correlated Response, Competition, and Female Canine Size in Primates

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ABSTRACT Recently, comparative analyses of female canine tooth size in primates have yielded two hypotheses to explain interspecific variation in female relative canine size. Greenfield ([1992] *Int. J. Primatol.* 13:631–657; [1992] *Yrbk. Phys. Anthropol.* 35:153–184; [1996] *J. Hum. Evol.* 31:1–19) suggested that covariation in male and female canine size across species indicates that female canine size reflects correlated response (in which the expression of a trait in one sex causes the expression of the same trait in the other sex). Plavcan et al. ([1995] *J. Hum. Evol.* 28:245–276) noted that female canine size in primates is associated with variation in categorical estimates of the intensity of female-female agonistic competition, suggesting that selection favors large female canine size in many species. While it may seem that the two models are in conflict, they are not. To simultaneously evaluate these two models, this analysis examines the joint relations between male canine size, female canine size, and estimates of female-female competition in a sample of 108 primate species. Overall, female canine size is correlated with variation in male canine size. Controlling for variation in male canine size, female canine size is also correlated with estimates of the intensity of female-female agonistic competition. The relation between these variables differs strongly between anthropoid and strepsirrhine primates. In anthropoids, the data suggest that selection for the development of large canines in females is not constrained by any affect of correlated response. In strepsirrhines, the evidence suggests that sexual selection may affect male canine size but that correlated response affects female canine size, resulting in monomorphism for most species. These observations help reconcile the observations of Greenfield ([1992] *Int. J. Primatol.* 13:631–657; [1996] *J. Hum. Evol.* 31:1–19) and Plavcan et al. ([1995] *J. Hum. Evol.* 28:245–276) and provide a more precise model for understanding interspecific variation in female canine size and hence canine dimorphism. *Am J Phys Anthropol* 107:401–416, 1998. © 1998 Wiley-Liss, Inc.

Commonly, primate canine tooth size sexual dimorphism is viewed as a product of sexual selection acting on males. Thus, selection favors big male canines because big canines help males to win fights for access to breeding females. A few studies recognize that female canine size is highly variable among species. Harvey et al. (1978) present evidence that female-female competition for

access to resources in large groups selects for large canine teeth, though data from Smith (1981) contradicts this. Lucas (1981) and Lucas et al. (1986) note that there is substantial variation in female canine size

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and suggest that this may be related to female competition but offer no comparative data to back this up.

More recently, two comparative analyses present apparently contradictory explanations for interspecific variation in primate female canine size. On the one hand, Plavcan et al. (1995) offer evidence that selection favors the development of large canine teeth in many female primates in association with female-female agonistic competition. On the other hand, Greenfield (1992b, 1996) presents evidence that interspecific variation in female canine size reflects correlated response to variation in male canine size.

Plavcan et al. (1995) suggest that, where females regularly engage in dyadic, agonistic contest competition, selection favors the development of relatively large canines for fighting, as long as there is a fitness consequence of winning and losing fights and large canines help females win fights. They also suggest that, where the outcome of escalated contests among females is regularly determined by alliances (or coalitions) of individuals rather than individuals fighting alone, selection for the development of weaponry is reduced. In support of this, they present evidence that female canines are small in species where female agonistic competition is either of low intensity or regularly occurs between coalitions of females and that female canines are larger in species where females compete intensely.

The correlated response model which Greenfield (1992b, 1996) favors may be unfamiliar to many readers. Lande (1980) presents a quantitative genetic model which predicts that, where traits are polygenic and autosomal, selection for the development of a trait in one sex should result in the expression of the trait in the other sex. This phenomenon is called *correlated response*. For example, if canine tooth size is determined autosomally and selection favors the development of large canine teeth in males, then females too should develop large canines, even in the absence of selection for large female canines. The model predicts that the primitive state for autosomally determined dimorphic traits should be monomorphism. Dimorphism should develop within a lineage only after a period of time,

pending that there is selective pressure to reduce the trait in the sex lacking selection to develop or maintain the trait (Lande, 1980). In the canine dimorphism example, the model predicts that after enlarged canine teeth were expressed in both males and females in the ancestral anthropoid lineage, canine dimorphism would subsequently evolve through a reduction in female canine size. This reduction in female canine size could be associated with the development of either sex-linked modifier genes that restrict the expression of the trait in females (Rice, 1984) or through the development of genes that alter the response of the development of the trait to sex hormones (Wright, 1993). Regardless of the exact genetic mechanism underlying this process, the model predicts that this phase in the evolution of dimorphism should be relatively slow, possibly requiring millions of generations (Lande, 1980). Furthermore, the Lande model predicts that if the trait is correlated between males and females, then selection against development of the trait in one sex could actually limit, or constrain, the expression of the trait in the other sex. In the canine dimorphism example, this latter phenomenon would suggest that the development of hypertrophied canines in some male primates could actually be limited by selection against the development of large canines in females.

Greenfield (1992b, 1996) presents evidence that interspecific variation in female canine size covaries with that of male canine size. He interprets this as evidence that correlated response explains most variation in female canine size and that selection for the development of canines as weapons operates in male primates but not females.¹ Plavcan et al. (1995) also find a correlation between male and female relative canine crown height but suggest that any effect of correlated response is secondary to that of selection for the development of female canines as weapons. They note that the wide-

¹In support of the correlated response model, Greenfield (1996) claims that Plavcan and van Schaik (1997a) (incorrectly cited as Plavcan and van Schaik, 1996) demonstrate no relation between relative female canine size and the female competition intensity classification. This citation is incorrect (see Plavcan et al., 1995); no such evidence was found, and no such claim has been made in any publication by Plavcan.

spread presence of canine dimorphism among anthropoid primates implies that the genetic control of male and female canine size is decoupled. Even so, unless male and female canine tooth size are under completely separate genetic control, some variation in relative female canine size may reflect correlated response. Finally, strepsirhines are characterized by relatively slight canine dimorphism, regardless of mating system (Kappeler, 1996). Correlated response, therefore, might explain the lack of canine dimorphism in strepsirhines.

The results of the studies of Plavcan et al. (1995) and Greenfield (1992a,b, 1996) appear contradictory. However, neither has evaluated the joint relation between male and female canine size and female agonistic competition in primates. Thus, the relative roles of selection for the development of weaponry and correlated response in the evolution of primate female canine size are unclear. Fortunately, each model generates testable predictions about the relation between relative male and female canine tooth size. This analysis therefore sets out to evaluate whether the models are in conflict and whether comparative evidence supports either or both models.

This analysis focuses only on these two models. Evaluation of other factors which may or may not be related to male or female canine size is beyond the scope of this analysis.

ASSUMPTIONS AND PREDICTIONS OF THE MODELS

The correlated response and intrasexual competition models make a variety of predictions about the relation between male and female canine size and estimates of female-female agonistic competition in primates. In order to define these predictions, we must first establish the appropriate measure of canine size or dimorphism.

The correlated response model specifically addresses the evolution of dimorphism over time within a lineage. It might seem best therefore to simply use a ratio estimate of dimorphism to evaluate correlated response. However, ratios cannot reveal whether a change in the magnitude of dimorphism results from a relative change in the value of the male or female trait. This is particularly

important for evaluating the female competition hypothesis, which specifically addresses the evolution of relative female canine size without regard to male canine size (Plavcan et al., 1995). Consequently, this study uses measures of relative male and female canine size derived as residuals from an allometric analysis.

A second problem is that the correlated response model refers only to the evolution of dimorphism within a single lineage. The dissociation of male and female canine size could theoretically proceed at different rates in different lineages. Ideally, the best way to test the correlated response model is to trace changes in male and female traits through a detailed fossil record (for an example of this type of analysis using peccaries see Wright, 1993). Consequently, a strong phylogenetic bias could be present in a cross-sectional analysis of extant species. For simplicity, the following analysis begins with the assumption that the initial dissociation of male and female canine size is a primitive trait for primates and that the rate that genetic control of male and female canine size was decoupled was the same in each lineage. This implies that any effect of correlated response is uniform among all species. The analysis of Greenfield (1992b, 1996) also implicitly makes this assumption. Further analyses were repeated within lower taxonomic groups to check for biases.

In the absence of any correlated response, the competition model predicts simply that species showing either low intensity or coalitionary agonistic female-female competition should be characterized by relatively smaller female canines than those showing high-intensity female-female competition (the definitions of competition are briefly presented below, and the reader is referred to Plavcan et al. (1995) for an extensive discussion of the definitions and classifications of female agonistic competition).

Figure 1 illustrates a series of predicted, idealized distributions of relative male and female canine size considering both the correlated response and competition models jointly. The panels show six hypothetical distributions of relative male and female canine tooth size (derived from a comparison to some measure of overall size), plotted on

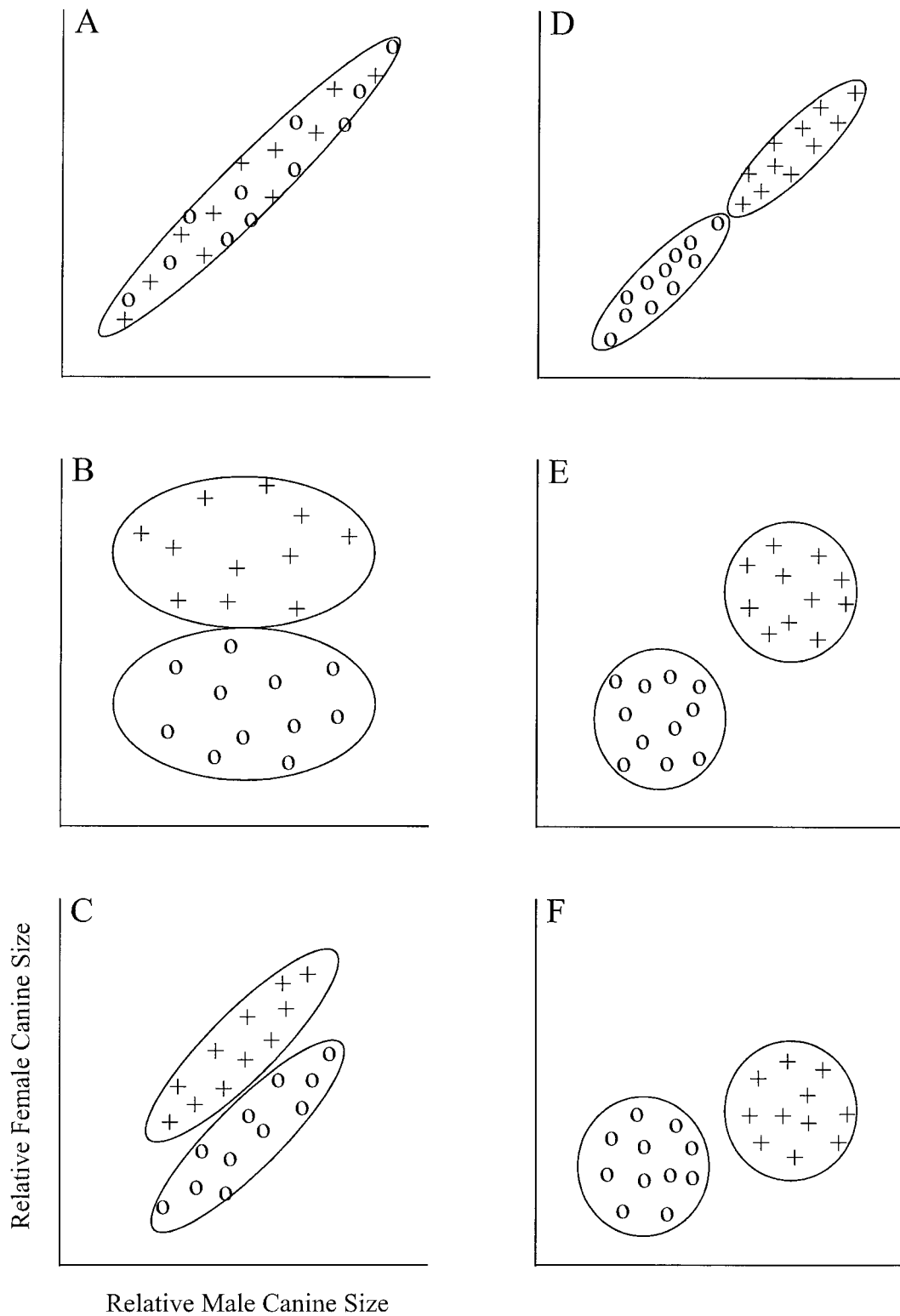


Figure 1. Six plots showing the predicted relation between male and female relative canine size and female behavioral classifications. Data and distributions are hypothetical. Crosses indicate species classified as high-intensity female-female competition, and zeros indicate species classified as low-intensity female competition. See text for a discussion of each plot.

the x - and y -axes, respectively. Points represented by a cross indicate high-intensity female-female agonistic competition species, and those represented by a circle indicate low-intensity female-female agonistic competition species.

Figure 1A shows the predicted distribution of species if correlated response is the only mechanism influencing female canine size. There should be a strong correlation between female and male canine size, with no clear relation between female canine size and the behavioral classifications. Note that the tight correlation depicted in Figure 1A implies either relatively uniform degrees of dimorphism among all species if the slope of the relation is isometric or a strong allometric effect on dimorphism if the slope deviates from isometry.

Figure 1B shows the predicted distribution of species if selection for the development of weaponry is the only mechanism influencing female canine size, with no correlated response. In this case, there is no correlation between male and female relative canine size, and the high-intensity female competition species have relatively larger canines than the low-intensity female competition species.

Figure 1C shows the predicted distribution of species if both mechanisms equally affect female canine size. Note that within each cluster corresponding to the competition classifications there is a strong correlation between male and female relative canine size. However, for any given male canine size, females classified as showing high-intensity competition have relatively larger canines than those classified as showing low-intensity competition.

Figure 1A–C assumes that there are no correlations between male and female intrasexual competition classifications and that there are no sexual differences in the strength of selection for the development of weaponry. Unfortunately, correlations between male and female behavior, as well as sexual differences in the relation between intrasexual competition and selection for the development of large canines, considerably complicate the predictions of the model. Figures 1D–F shows predicted distributions of relative male and female canine size

assuming strong covariation between male and female competition classifications (i.e., in each species males and females are both classified with either high-intensity or low-intensity competition).

Figure 1D shows a predicted distribution of species if there is a perfect correlation between classifications of male and female competition and correlated response affects female canine size. Note that there is a strong correlation between male and female canine size both across the competition classifications and within them. This suggests that correlated response plays an important role in the development of female canine size. Note that if the analysis were limited to female canines only (a univariate analysis of female canine size on the y -axis), we would conclude that the high-intensity females have relatively larger canines than low-intensity females, possibly erroneously corroborating the competition hypothesis. On the other hand, this pattern could spuriously corroborate the correlated response model if selection associated with the male and female competition classifications was identical in nature and was perfectly correlated across taxa (see Leroi et al., 1994). This latter situation seems unlikely but cannot be ruled out completely.

Figure 1E shows the predicted distribution of species if classifications of male and female behavior are the same but correlated response does not operate. The key observation here is that there is no correlation between male and female relative canine size within the female competition classifications. Therefore, the position of the distributions probably reflects only an interaction between male and female behavior, and correlated response probably plays little role in determining female canine size (though it cannot be ruled out entirely).

Finally, Figure 1F shows the predicted distribution of species similar to Figure 1E, but in this case the effect of selection for the development of weaponry is unequal between the sexes. In this example, high-intensity male-male competition is associated with large increases in relative male canine size, while high-intensity female-female competition is associated with only modest increases in female canine size. Con-

sequently, the high-intensity female cluster is shifted to the right in the plot.

The above hypotheses can be tested in a relatively straightforward fashion using simple correlation and regression analyses.

MATERIALS AND METHODS

Data

Data on average male and female maxillary canine crown height for 108 species were taken from Plavcan (1990) for anthropoid primates and Kappeler (1996) for strepsirrhine primates. Among canine dimensions, maxillary canine crown height is most strongly correlated with male and female behavioral variables (Plavcan, 1993; Plavcan and van Schaik, 1992; Plavcan et al., 1995; Greenfield, 1992a,b,c, 1996). Further details of the exact measurements and samples of species measured are presented in Plavcan (1990), Plavcan and van Schaik (1992), and Plavcan et al. (1995).

Adult body mass data were abstracted from Plavcan and van Schaik (1997b) and Smith and Jungers (1997). These two sources present body mass data on wild-caught specimens abstracted from the primary literature. Data on M/1 tooth lengths were available only for the anthropoid sample (Plavcan, 1990).

Measurement of relative canine size

The measurement of relative male and female canine size for the purposes of this analysis presents a difficult problem. A straightforward regression of female against male canine size might seem logical, but such a procedure is confounded by interactions between male canine size, male body size, male intrasexual agonistic competition, and phylogeny (see Greenfield and Washburn, 1991; Mitani et al., 1996; Plavcan, 1993; Plavcan and van Schaik, 1992, 1997b). A majority of the species showing the highest degrees of male-male competition and the largest canines are also the largest species. Monomorphic species, on the other hand, occur across a wide range of body sizes. This results in a skewing of the primate distribution at the large end of the size range when female canine size is plotted against male canine size (Fig. 2). Conse-

quently, variation in a residual measure of female canine size derived from a direct regression against male canine size will reflect primarily variation in male canine size in dimorphic species. Therefore, male canine size alone is a poor baseline from which to establish an allometric criterion of subtraction for measuring relative female canine size.

Instead, male and female relative canine sizes were estimated as the least-squares residual deviation from an isometric line passed through a comparison of canine size to either body mass or the mesiodistal length of M/1. In both cases, the isometric line was passed through pooled male and female data sets, treating males and females as independent points (i.e., both males and females were compared to the same isometric line). The isometric line is preferred over an empirical line following the recommendations of Smith (1980), Plavcan (1993), and Plavcan et al. (1995) and corresponds to a simple ratio of canine size and the independent variable.

Behavioral classifications

Classifications of male and female intrasexual competition were taken from Plavcan et al. (1995), to which the reader is referred for detailed definitions and discussion. In short, agonistic, escalated competition (fighting) in either males or females is classified on the basis of intensity, potential frequency, and context (coalitionary competition).

The intensity and potential frequency categories are dichotomized into high and low classes. High-intensity and high-frequency species are predicted to have larger canines than low-intensity and low-frequency species, respectively.

High-intensity contest competition is recognized when either adults are intolerant of one another or stable dominance hierarchies are maintained through agonistic interactions. Low-intensity competition is recognized when individuals are reported to be tolerant of one another, dominance hierarchies are difficult to detect, and escalated intrasexual competition is reported as rare or absent. To render the analysis conservative, a sex of a species was classified as high intensity whenever escalated agonistic com-

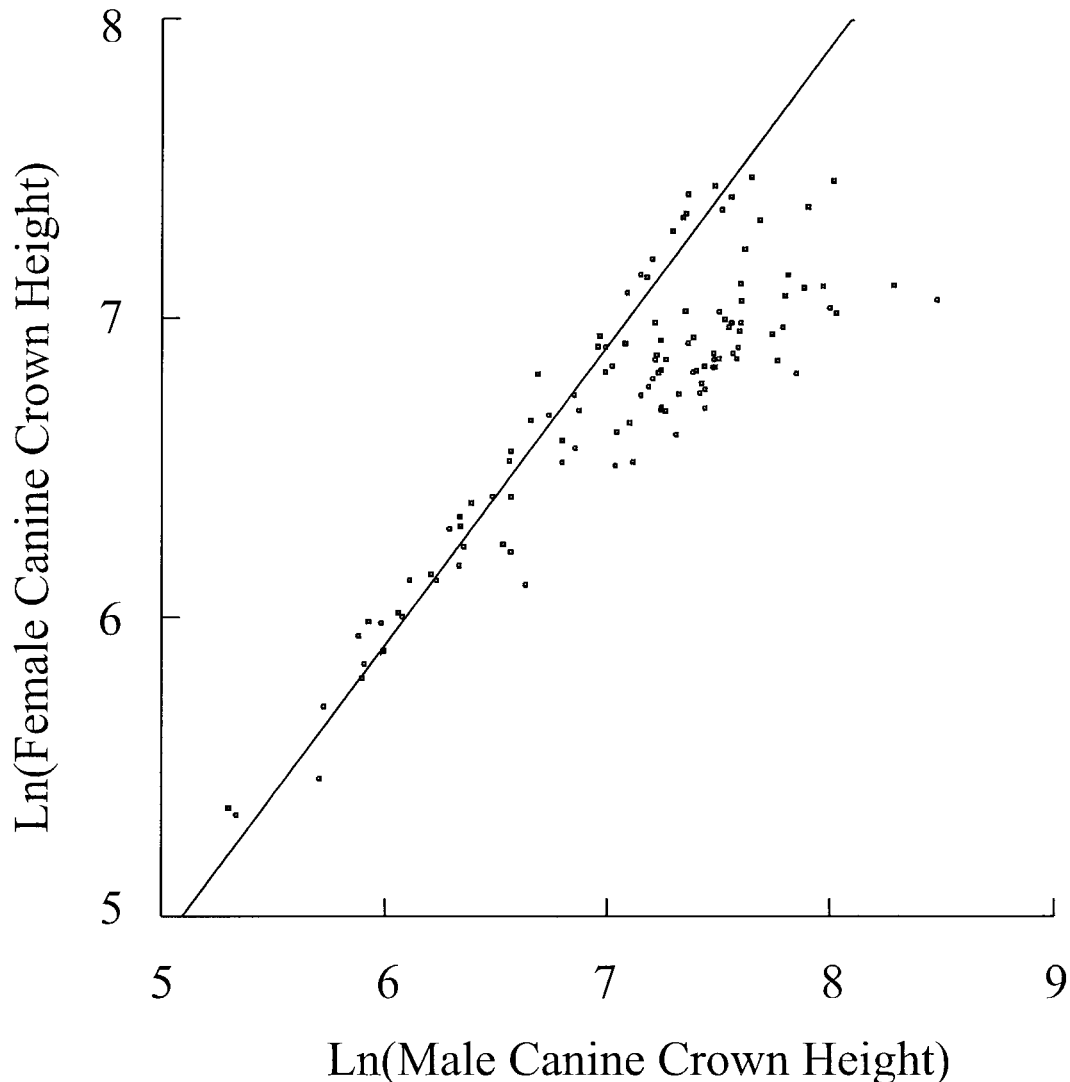


Figure 2. Bivariate plots of ln-transformed male and female maxillary canine crown height for 108 species of primates. An isometric line is fitted through monomorphic species.

petition was reported as common among adults of the same sex. High-frequency competition is recognized when more than one adult of a sex typically occurs in a group, while low-frequency competition is recognized when only one adult of a sex typically occurs in a group.

Plavcan et al. (1995) hypothesize that when agonistic competition regularly occurs between alliances, or coalitions, of individuals, selection for the development of weaponry should be reduced in comparison to the

situation where the outcome of contests is determined by individuals acting alone. This is based on the hypothesis that, where competition occurs between groups of individuals, the number of individuals enlisted in a coalition will be as important, if not more so, than individual weaponry in determining the outcome of contests. Such coalitionary competition is rare among males but common among female anthropoids.

The coalitionary competition category is divided into coalitions present (coalitionary

competition) or absent (noncoalitionary competition). Males or females of species showing coalitionary competition are specifically predicted to have relatively smaller canines than high-intensity, high-frequency competition species. Notably, the males of several species are classified as showing coalitionary competition. These species show coalitionary competition only in between-group conflicts and otherwise would be classified as showing low-intensity competition (Plavcan et al., 1995). The classification of these species as coalitionary renders any test of the coalitions hypothesis conservative.

Behavioral classifications are not available for the entire data set. Therefore, whereas the correlation between male and female canine size can be evaluated for all 108 samples, there are only 66 species for which competition classifications are available for either or both males and females. For a number of species, behavioral classifications could be made for only one sex. Thus, sample sizes vary among the analyses.

Plavcan et al. (1995) demonstrate that, while relative male canine size is associated with variation in all three competition types, relative female canine size is significantly associated only with the intensity and context of competition but not the frequency. For this reason, the analysis presented below considers only the effects of female competition intensity and context on relative female canine size.

Data analyses

Data analysis is presented in two stages. First is a straightforward test of the hypothesis that male and female canine size are correlated. The analysis is carried out for all species values and controlling for phylogenetic effects. Phylogeny is controlled in two ways: first by reanalyzing data in progressively lower taxonomic groups and, second, using the phylogenetic contrasts method (Felsenstein, 1985; Pagel and Harvey, 1988; Pagel, 1992), following the algorithms and recommendations set forth in Pagel (1992) and setting branch lengths equal to 1 in the absence of reliable data on branch lengths. Phylogenetic contrasts were calculated by hand. Phylogenies used for the analysis were drawn from Purvis (1995). Unresolved

nodes in the Purvis phylogeny were resolved using phylogenies or taxonomies from Napier (1985) for *Presbytis* and Rumpler and Dutriaux (1986) for lorises and galagoes. Phylogenetic contrasts were also calculated using phylogenies for papionines from Strasser and Delson (1987), for cercopithecines from Ruvolo (1988), for platyrrhines from Ford (1986), Kay (1990), Rosenberger (1981), and Schneider et al. (1993), and for strepsirrhines from Rumpler and Dutriaux (1986) and Stanger and Macedonia (1992). Results did not differ substantially using the alternative phylogenies.

Next the pattern of male and female relative canine tooth size is evaluated against the predictions of the correlated response and selection models outlined in Figure 1 (see above). Phylogenetic control was difficult in these analyses. Meaningful statistics could not be generated for phylogenetic contrasts because variation in male and female behavioral classifications did not allow enough meaningful contrasts between nodes within the phylogeny. Reanalysis of the data within lower taxonomic levels was, for the most part, limited by small sample sizes. The lack of strong phylogenetic control in the analysis of the behavioral correlations means that phylogeny cannot be ruled out as a potentially confounding factor.

RESULTS

Correlation between male and female canine size

Across the whole primate sample, ln-transformed estimates of male and female canine size are strongly correlated with one another ($N = 108$, $r = 0.909$, $P < 0.001$) (Fig. 2). This is not surprising because of the large range of overall sizes encompassed by the sample.

Both measures of residual canine crown height show strong correlations between male and female values (Table 1; Fig. 3). The only large samples showing no correlation between male and female residual canine size are cercopithecines ($N = 26$), but only for residuals derived from a comparison to body mass, and colobines ($N = 18$), but only for residuals derived from a comparison to M/1 size. Two small samples also fail to achieve statistical significance (hylobatids

TABLE 1. Correlations between female and male residual canine size

	Body mass residuals ¹			M ₁ residuals ²		
	N	r	P	N	r	P
All primates	108	0.573	<0.001	—	—	—
Strepsirrhines	31	0.927	<0.001	—	—	—
Lorisids	13	0.856	<0.001	—	—	—
Lorisines	6	0.986	<0.001	—	—	—
Galagines	8	0.819	0.013	—	—	—
Lemurids	18	0.938	<0.001	—	—	—
Lemurines	11	0.815	0.002	—	—	—
Indriids	3	0.999	0.027	—	—	—
Cheirolgals	3	0.998	0.041	—	—	—
Anthropoids	77	0.649	<0.001	79	0.554	<0.001
Catarrhines	54	0.647	<0.001	57	0.404	0.002
Cercopithecoids	44	0.607	<0.001	47	0.524	<0.001
Cercopithecines	26	0.278	0.169	29	0.449	0.015
Colobines	18	0.712	0.001	18	0.393	0.107
Hominoids	10	0.969	<0.001	10	0.950	<0.001
Hylobatids	5	0.155	0.803	5	0.176	0.777
Great Apes	5	0.987	0.002	5	0.968	0.007
Platyrrhines	23	0.761	<0.001	22	0.814	<0.001
Cebines	19	0.809	<0.001	18	0.817	<0.001
Callitrichids	4	0.989	0.011	4	0.927	0.073

¹ Least-squares residuals from an isometric line passed through the pooled male and female data on maxillary canine crown height and body mass.

² Least squares residuals from an isometric line passed through the pooled male and female data on maxillary canine crown height and the mesiodistal length of the mandibular first molar. Molar tooth data was not available for the strepsirrhines.

(N = 5) and callitrichids (N = 4), but the latter only for residuals from the comparison to M/1 length).

The phylogenetic contrast method yields a correlation of $r = 0.668$ (N = 92) for the comparison of male and female residual canine size. This correlation is stronger than that derived for the species values and demonstrates that the correlation between male and female canine size is not a taxonomic artifact. The sample size is less than 108 because of unresolved nodes in the phylogeny.

Joint effect of female competition and male canine size

There is a strong interaction between male and female competition classifications (Table 2). Specifically, because the males of most anthropoid species are classified as showing high-intensity competition, most anthropoid species classified as showing high-intensity female competition also show high-intensity male competition. Consistent with this observation, species classified as showing either high-intensity or coalitionary female competition show significantly greater relative male canine size than those characterized by low-intensity female competition (Table 3). This interaction between

male and female competition classifications means that the relations between male and female canine size and female competition classifications should resemble the distributions in Figure 1D–F.

Male and female relative canine size are correlated in the low-intensity female competition classification (Table 4) using residuals derived from either a comparison to body mass or M/1 size but are correlated within coalitionary species using only residuals derived from a comparison to M/1 size. Within the high-intensity competition classification, there is no significant correlation between male and female relative canine size using either set of residuals.

Considered separately, anthropoids and strepsirrhines display very different distributions (Fig. 4). Figure 4A shows the anthropoid distribution of male and female residual canine size (derived from a comparison to body mass), with a reduced major axis (RMA) regression line passed through the low-intensity female competition species. Note first that there is a strong correlation between male and female residual canine size within the low-intensity female competition species but none in the high-intensity or coalitionary female competition species (this is the reason the RMA line is passed only

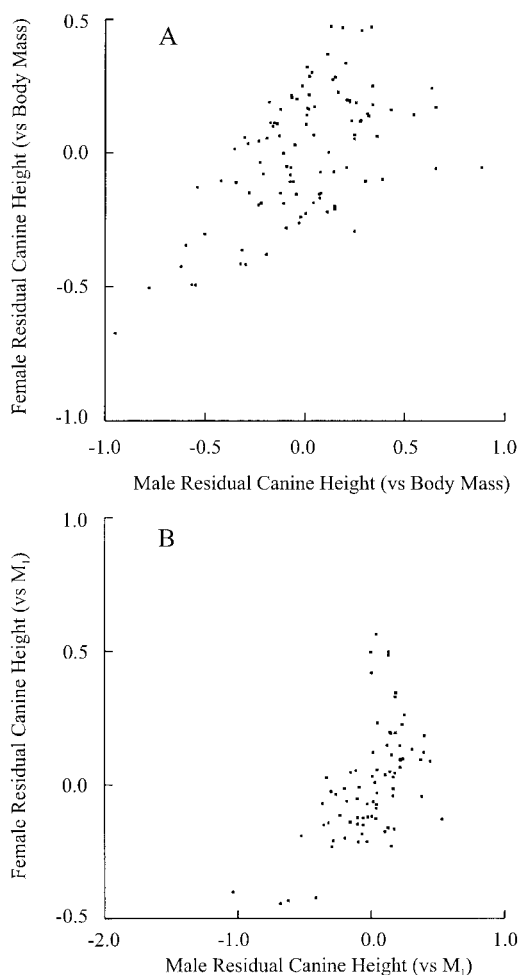


Figure 3. Bivariate plots of relative male and female canine size in primates. **A:** Residuals derived from a comparison of ln-transformed male and female maxillary canine crown height to an isometric line using body mass as the independent variable. **B:** Residuals derived from a similar comparison as A, except mandibular molar tooth mesiodistal length was substituted for body mass as the independent variable.

through the low-intensity species). Next note that the high-intensity female competition species fall above the RMA line, while the majority of coalitionary female competition species fall below the line. ANOVA of residual values derived from the RMA regression line corroborates this visual evaluation (Table 5). These results suggest that within the low-intensity species, relative female canine size strongly covaries with male canine size. Within the high-intensity species,

TABLE 2. Matrices of male (rows) and female (columns) intrasexual competition intensity classifications within taxonomic groups¹

	All primates		Anthropoids		Prosimians	
	LI	HI	LI	HI	LI	HI
LI	26	3	3	3	23	0
HI	20	29	18	25	2	4

¹ HI, high intensity; LI, low intensity.

TABLE 3. ANOVAs for differences in relative male canine size (residuals derived from a comparison to male body mass) among species of different female competition classifications¹

Effect	SS	DF	MS	F	P
Anthropoids					
LI vs HI	0.860	1	0.860	13.528	0.001
Error	2.161	34	0.064		
LI vs Coal.	1.542	1	1.542	23.801	<0.001
Error	2.073	32	0.065		
HI vs Coal.	0.108	1	0.108	2.272	0.144
Error	1.240	26	0.048		
Strepsirrhines					
LI vs HI	0.320	1	0.320	6.554	0.016
Error	1.320	27	0.049		

¹ Coal., coalitionary female competition; HI, high-intensity female competition; LI, low-intensity female competition.

TABLE 4. Correlations between residual maxillary canine crown height of females and males within different classifications of female intrasexual competition¹

Female classification	N	r	P
Residuals from a comparison to body mass			
Coalitions	13	0.475	0.101
LI	46	0.686	<0.001
HI	19	0.231	0.342
Residuals from a comparison to M₁ size			
Coalitions	13	0.657	0.015
LI	20	0.656	0.002
HI	15	0.334	0.224

¹ HI, high intensity; LI, low intensity.

female canine size does not covary with male canine size, and females have relatively larger canines than low-intensity females for any given male canine size. The coalitionary species have relatively small canines compared to the high-intensity species.

Figure 4B shows the strepsirrhine distribution, again with an RMA regression line passed through the low-intensity female competition species. Unlike the anthropoids, there is a significant correlation between male and female canine size in both the low- and high-intensity competition species, and

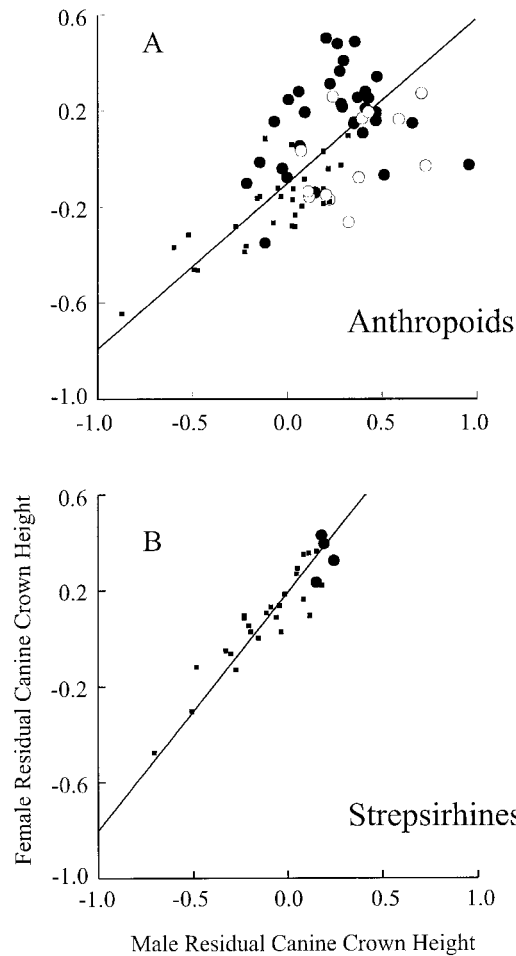


Figure 4. Bivariate plots of residual female vs. residual male maxillary canine crown height in anthropoids (A) and strepsirhines (B). Small squares represent species classified as showing low-intensity female competition, open circles represent species classified as showing high-intensity female competition, and filled circles represent species classified as showing coalitionary female competition. The line in each panel is a reduced major axis line passed through the low-intensity female competition species.

the high-intensity female competition species fall close to the regression line. This distribution closely resembles that predicted in Figure 1D. ANOVA of residual values derived from the regression line shows no significant difference between high- and low-intensity female competition species (Table 5). This suggests that variation in relative female canine size in strepsirhines covaries with that of the males.

TABLE 5. ANOVAs for differences in relative female canine size (measured as a residual from a RMA line passed through the low-intensity female competition species in a comparison of relative female canine size vs. relative male canine size) between female competition classifications¹

Effect	SS	DF	MS	F	P
Anthropoids					
LI vs. HI	0.313	1	0.313	11.199	0.002
Error	0.949	34	0.028		
LI vs. Coal.	0.108	1	0.108	5.379	0.027
Error	0.642	32	0.026		
HI vs. Coal.	0.647	1	0.647	16.311	<0.001
Error	1.032	26	0.040		
Strepsirhines					
LI vs. HI	0.005	1	0.005	0.622	0.437
Error	0.226	27	0.008		

¹ Coal., coalitionary female competition; HI, high-intensity female competition; LI, low-intensity female competition.

DISCUSSION

The results of this analysis provide corroborative evidence that variation in female canine size among primates is a function of both correlated response and selection for the development of weaponry in females. However, anthropoids and strepsirhines differ strongly in the pattern of covariation between relative male and female canine size and the behavioral classifications used here. This suggests that the relative influence of correlated response and selection for the development of female weaponry differs strongly between these two groups.

Strepsirhines

Interspecific variation in strepsirhine relative female canine size appears to reflect correlated response. This is not surprising, since all strepsirhines are characterized by nearly monomorphic canines (Kappeler, 1996), even though relative canine size varies among species. For example, even though *Varecia variegata* have large projecting canines and *Propithecus diadema* have short canines, both species are nearly monomorphic.

A clear explanation for strepsirhine monomorphism has so far evaded comparative analyses (Kappeler, 1996). Kappeler (1996) found no relation between variation in strepsirhine canine dimorphism and a series of behavioral/ecological variables. In fact, Kappeler found that only phylogeny correlates with the relatively modest variation in strep-

sirhine canine dimorphism. Kappeler went on to suggest that sexual selection may not favor the development of traits such as large body size or canine size to help males win fights, because male reproductive success depends on mechanisms other than physical combat.

Plavcan et al. (1995) found that female strepsirhines ranked as showing high-intensity competition tend to have relatively larger canines than those ranked as low-intensity. However, the analysis presented here suggests that this result may be an artifact of the covariation in male and female intensity classifications: where females are classified as high intensity, so too are males.

It is important to note that male strepsirhines classified as showing high-intensity competition have significantly larger relative canine size than those classified as showing low-intensity competition (ANOVA, $F = 4.839$, $P = 0.037$). This result holds using phylogenetic contrasts (in all five pairwise contrasts between high- and low-intensity males, the high-intensity species has larger canines). The fact that male canine size is correlated with the male-male competition classifications suggests, contra Kappeler (1996), that sexual selection from physical combat might favor the development of big male canines. If true, then correlated response might act as a constraint on the evolution of canine dimorphism in strepsirhines. This is the first analysis to provide evidence that sexual selection may affect male canine size in strepsirhines and at the same time to suggest a mechanism to explain why strepsirhine canines are nearly monomorphic.

This interpretation for strepsirhine canine monomorphism is still uncertain. In the first place, strepsirhine behavior is relatively poorly known, and any of the competition classifications used here may change with the advent of better data. Furthermore, because male and female competition classifications are the same in almost all strepsirhine species, the covariation in relative male and female canine size may reflect equal selective pressures on canine size. While perhaps less likely than the correlated response model, this possibility cannot

yet be discounted (for a discussion of the potential inability of comparative analysis to distinguish between such hypotheses see Leroi et al., 1994). Finally, left unanswered are why the genetic control for male and female canine size in strepsirhines has not decoupled, as in anthropoids and whether the lack of body mass dimorphism in strepsirhines is also a function of correlated response. Such analyses are beyond the scope of this paper.

Anthropoids

The results of this analysis are consistent with the hypothesis that anthropoid relative female canine size is at least partially a function of both selection for the development of weaponry and correlated response. Unlike the strepsirhine distribution, which neatly fits into the predictions of Figure 1D, the anthropoid pattern of male and female relative canine size is complex and appears to reflect a hybrid of the predictions of Figure 1C–E.

In the first place, it is notable that the low-intensity female competition species show a very strong correlation between male and female relative canine size, suggesting that correlated response explains much of the interspecific variation in these species. In stark contrast, the high-intensity and coalitionary female competition species show no correlation between relative male and female canine size. This seems to suggest that within the high-intensity and coalitionary female competition species, correlated response does not explain variation in relative female canine size.

The next question to address is whether the high-intensity and coalitionary competition females have relatively larger or smaller canines for any given male canine size than the low-intensity females. The lack of correlation between male and female canine size in two of three competition classifications precludes the use of analysis of covariance to test this hypothesis. Instead, we must make the comparison using an RMA regression line passed through the low-intensity distribution (use of a least-squares line does not alter the results). As shown in Figure 4A and Table 5, the high-intensity species fall above the line, and the coalitionary species fall

below it. This suggests that indeed the high-intensity female species have relatively larger canines than the low-intensity female species for any given male canine size. Furthermore, as predicted by Plavcan et al. (1995), the coalitionary species have relatively smaller canines than the high-intensity species.

On the whole, these results suggest that correlated response does not operate in conflict with selection for the development of weaponry in female anthropoids. It appears that in the absence of selection for the development of weaponry, correlated response is an important factor influencing the expression of anthropoid female canine size. However, if there is selection for the development of weaponry, correlated response plays little part in explaining interspecific variation in female canine tooth size. Thus, in anthropoids, unlike in strepsirhines, correlated response does not seem to constrain the evolution of female canine size. This result is, of course, consistent with the presence of strong canine dimorphism in many anthropoids. Interspecific variation in dimorphism alone proves that male and female canine size can vary at least partly independently in anthropoids. Thus, correlated response should not be expected to constrain the development of large canines as weapons in some females. The analysis provides evidence that at least some variation in canine dimorphism reflects selection acting on female canine size (Plavcan et al., 1995; Harvey et al., 1978; Lucas et al., 1986).

Problems with the models

The results of this analysis must be tempered with a careful consideration of the shortcomings of the behavioral classifications, the weakness of comparative analysis for differentiating between genetic and non-genetic mechanisms affecting character evolution, and the fact that the correlated response model is best tested using data within a single lineage rather than across lineages.

The classifications of female and male competition used in this analysis sacrifice precision in order to allow a broad comparative analysis (Plavcan et al., 1995). Important variation in both male and female

behavior is subsumed within the behavioral classifications. More refined evaluations of the relation between behavior and morphology may reveal other mechanisms that affect both male and female canine size or may refine our understanding of the selective pressures underlying variation in canine dimorphism.

Leroi et al. (1994) argue that comparative analyses, such as those used here, cannot distinguish between competing evolutionary genetic models for the evolution of traits. For example, as noted above, the pattern of variation in strepsirhine relative canine size cannot distinguish between the correlated response model and the hypothesis that there is equal selective pressure on male and female canine size. For reasons noted above, the former seems a more likely hypothesis. Nevertheless, the results of this analysis only corroborate or refute the predictions of the two recently proposed models and do not in themselves offer proof that either correlated response or selection affect female canine size. Furthermore, where covariation in female and male canine size is posited to be a result of correlated response, the exact genetic mechanism determining male and female covariation in canine size is open to question, because the analysis evaluates only whether male and female canine sizes covary. Thus, while the results of these analyses offer corroborative evidence for the models, they certainly do not offer proof and should not be taken as definitive evidence for the operation of either correlated response or selection for the development of weaponry in females.

As mentioned previously, the correlated response model specifically addresses the evolution of sexual dimorphism through time within a lineage. Consequently, the best test for the model would be to trace the evolution of canines in males and females through time, demonstrating first the hypertrophy of the canines in both sexes and then the subsequent reduction of canines in females. The fossil record for most extant species is too poor to allow such a test.

Instead, Greenfield (1992b, 1996), Plavcan et al. (1995), and this analysis address only the hypothesis that interspecific varia-

tion in female canine size covaries with interspecific variation in male canine size. It is reasonable to suppose that covariation in male and female canine size across species reflects correlated response, but, as just noted above, neither the mechanism underlying this covariation nor the exact degree to which correlated response actually influences canine size in any particular species can be demonstrated by this analysis.

Unless the genetic control of male and female canine size decoupled in the common ancestor of all anthropoids and the effect on female canines is uniform across all anthropoids, we should expect different effects of correlated response in different lineages. For example, there is an obvious difference in the covariation between male and female canine size between strepsirhines and anthropoids. Likewise, even though this analysis suggests that there is an effect of correlated response within anthropoids, at the same time female canines in most anthropoids are obviously smaller than those of males. Thus, female canine size in most species should reflect a balance between shared genetic control of male and female canine size, the mechanism that decouples this control and allows canine reduction in females, and selection for canine reduction or increase in females. Obviously, the evolution of these features could proceed differently in different lineages.

If an effect of correlated response did vary widely among different lineages, then we might expect either a lack of correlation between male and female canine size across lineages regardless of competition classifications or at least taxonomic variation in the relation between male and female canine size. Obviously, the strong correlation between male and female canine size in both strepsirhines and low-intensity female competition anthropoids proves that the first point is not true. At the same time, the difference between strepsirhines and anthropoids suggests that there are indeed taxonomic differences in the expression of correlated response. However, within the anthropoid distribution, there is still little indication that any of the results are an artifact of phylogeny. Within the low-intensity female competition species, there is a

mix of hominoids, platyrrhines, cercopithecines, and colobines, with no clear taxonomic differences in the relation between male and female canine size. Within the high-intensity species, these taxa are also represented. Cercopithecine males tend to have hypertrophied canines, creating a taxonomic difference in relative male canine size (Plavcan, 1993), but this is not repeated for relative female canine size. Within cercopithecines, there is still no correlation between male and female canine size within the high-intensity female competition species. Thus, it does not appear that the results of this analysis are an artifact of variation in the effect of correlated response across taxa. Even so, only an analysis of changes in canine size through time within different lineages can directly address this problem.

Finally, it should be emphasized that this analysis tests broad hypotheses about the influence of two factors on the evolution of relative female canine size in primates. This does not by any means exclude other factors from being important in the evolution of male or female canine size, either across species or within individual lineages. For example, other studies have suggested that across species relative male canine size is influenced by predation pressure (e.g., Leutenegger and Kelley, 1977; Plavcan and van Schaik, 1992). It is widely held that both male and female pithecine canines are morphologically specialized for opening hard fruit (e.g., Greenfield, 1992b; Plavcan and Kelley, 1996). The goal of this analysis is not to explain variation in all species by two isolated factors, and the results should not be interpreted this way. Rather, the goal is to evaluate whether interspecific variation in relative female canine size is consistent with either or both hypotheses. With the results presented here, there is still a large amount of variation in relative male and female canine size that is unexplained.

Phylogenetic implications

Recently, Kay et al. (1997) noted that canine tooth size sexual dimorphism is probably a derived character for anthropoid primates. This view is not new, and canine dimorphism has been used as evidence that

early cercopitheciine adapiforms gave rise to anthropoid primates (e.g., Gingerich, 1995; Simons and Rasmussen, 1996). Conversely, Lucas et al. (1986) suggested that early anthropoids were characterized by small canines in both sexes. They suggested that initially sexual selection favored the evolution of hypertrophied male canines, with phylogenetic inertia maintaining large male canine size in descendent anthropoids.

The correlated response model makes several predictions about dimorphism in early anthropoids pertinent to these views. In the case of the canine teeth, Lande's (1980) model clearly predicts that sexual selection for large male canines initially should result in the hypertrophy of both male and female canines. Thus, the primitive condition should be analogous to that seen in, for example, *Lemur catta*, not a condition like *Callicebus* in which both males and females have small canines. Dimorphism should evolve only later by reduction of the female trait (this does not mean that male canines cannot be further enlarged or reduced). If this model is true, then canine reduction in female anthropoids might be the shared derived character among anthropoids, not necessarily dimorphism arising through hypertrophy of the male canine.

It is well known that a number of adapid primates show substantial canine dimorphism (Krishtalka et al., 1990; Gingerich, 1981, 1995; Simons and Rasmussen, 1996). Conversely, canine dimorphism has not been documented in Omomyid primates. If Omomyids are the sister taxon to anthropoids (Kay et al., 1997), then this might constitute evidence that canine dimorphism has evolved in parallel in at least two primate lineages.

This model also suggests that the enlarged canines of some female anthropoids, including hylobatids, callitrichids, and several subspecies of *Colobus guereza*, are secondarily derived (see Lucas et al., 1986). *Colobus guereza* is particularly interesting. Variation in female canine size among the subspecies of this species is tremendous, with *C. g. occidentalis* possessing nearly hylobatid-like canines (Hayes et al., 1995; Lucas et al., 1986). Regardless of the underlying mechanisms driving the evolution of large canines in female *C. guereza* (Hayes et

al., 1995), the fact that there is large variation in female canine size without parallel variation in male canine size suggests that any effect of correlated response in this species does not constrain the evolution of female canine size.

CONCLUSIONS

Two hypotheses have recently been forwarded to explain interspecific variation in female canine size in primates: correlated response to male canine size (Greenfield, 1992b, 1996) and selection for the development of weaponry in females (Plavcan et al., 1995). The operation of these two mechanisms is not mutually exclusive, and the results of this analysis suggest that both mechanisms operate simultaneously in anthropoid primates. When male canine size was controlled for, females classified by Plavcan et al. (1995) as showing high-intensity, noncoalitionary competition show relatively large canine size, with no correlation between male and female canine size. Conversely, those females classified as showing either low-intensity agonistic competition or coalitionary competition possess on average relatively small canines as compared to high-intensity female competition species. Within the low-intensity female-female competition classification there is a strong correlation between female and male relative canine size. This suggests that, overall, correlated response is important in explaining female canine size only in those species where there is little or no selection for the development of weaponry.

Among strepsirrhines (which show low degrees of canine dimorphism), male and female relative canine sizes are strongly correlated. At the same time, male canine size is correlated with intensity of male-male competition. This suggests that sexual selection may favor the development of large canines in some male strepsirrhines, while at the same time the expression of canine dimorphism is constrained by correlated response.

This analysis reconciles the seemingly conflicting findings of Greenfield (1992a,b) and Plavcan et al. (1995), demonstrating that both models are probably partially correct.

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